

# 苔草属复序苔草亚属十四种植物叶片的解剖学研究\*

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## LEAF ANATOMY OF FOURTEEN SPECIES IN CAREX SUBGENUS *INDOCAREX* (CYPERACEAE)

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**Abstract** Among the subgenera of the genus *Carex*, the subgenus *Indocarex* has been seldom studied in any respects. Its systematic position and its subdivision are still disputable. Leaf anatomy of 14 species in the subgenus *Indocarex* from China was studied. The anatomical characters are proved to be systematically valuable. (1) Characters of lamina transverse section; All leaves of these 14 species are dorsiventral. The outline mostly V-shaped, occasionally flat or nearly flat, with adaxial lateral rib in each half of lamina and some of them flanged. The cells of adaxial surface larger than those of abaxial surface, and the epidermal cells over veins usually smaller than others. Air-cavities between vascular bundles are well developed, and bulliform cells also well developed in most taxa. The vascular bundles are collateral, bundle sheaths double-layered, and the outer sheath parenchymatous and the inner sheath fibrous. (2) Characters of lamina epidermis; The shape of the cell on both surfaces is generally rectangular, and the anticlinal wall of epidermal cell sinuous; stomata is paracytic, elliptic to oblong, rarely sub-circular; prickles occur on adaxial surfaces of certain species; papillae are only obvious on abaxial surface of *C. moupinensis* Franch. The characters of transverse section and epidermis of leaf blades of these 14 species differ from each other to certain degree, and closely related species are similar in anatomical characters. The anatomical characters of lamina are of value for classification at specific and sectional level of the subgenus *Indocarex*. Despite of the variation of these characters among species, a certain number of characters appears to be shared by the members of the subgenus, and some of the common characters are primitive. In addition, some gross morphological characters are common and primitive also. Therefore, the subgenus *Indocarex* may be primitive in the genus *Carex*. The anatomical and morphological characters of *C. scaposa* C. B. Clakre and *C. densifimbriata* Tang et Wang ex S. Y. Liang are distinct. The two species and their allies should be treated as section instead of subsection. The three species in the section *Polystachyae* share some anatomical characters and comprise a coherent group.

**Key words** *Carex*; Subgenus *Indocarex*; Leaf; Transverse section; Epidermis

**摘要** 选择中国复序苔草亚属 6 组 4 亚组的代表植物 14 种,进行了叶片解剖学研究,观察了其横切面和表皮特征,证明上述特征在各类群之间存在差异,具有一定的系统学意义。这 14 种植物叶片的横切面和表皮都具有有一些原始的性状,表明复序苔草亚属中的植物可能在苔草属中是较原始的。在所观察的植物中, Sect. *Polystachyae* 植物叶片解剖学特征比较一致,说明此组的建立比较合理;而 Sect. *Indicae*

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组已有明显分化,尤其是 *Carex scaposa* C. B. Clarke 和 *C. densifimbriata* Tang et Wang ex S. Y. Liang 与其它植物明显不同,而且其外部形态特征在复序苔草亚属中也比较独特,因此赞成将它们及其近缘类群做为一个组而非亚组。

**关键词** 苔草属;复序苔草亚属;叶片;横切面;表皮

苔草属 *Carex* 是莎草科 Cyperaceae 中最大的属,也是被子植物中最大的属之一,约 2000 多种(Airy Shaw, 1973),广布全世界,我国有 500 种左右。该属的分类历来被视为难题。Kükenthal(1909)在其世界性苔草亚科专著中把该属分为 4 个亚属,其中原始苔草亚属 Subgen. *Primocarex* 和复序苔草亚属 Subgen. *Indocarex* 是否为自然的类群,以及它们在属中的系统位置一直颇有争议。现在一般认为原始苔草亚属是人为类群,并不原始,是另外两个亚属(苔草亚属 Subgen. *Carex* 和二柱苔草亚属 Subgen. *Vigneae*)中不同组的进化类型的组合(Reznicek, 1990; Nelmess, 1952; Kreczetowicz, 1936),本文作者赞同这种观点。但关于复序苔草亚属,目前仍缺乏深入研究,还存在不同意见;而且 Raymond (1959)和 Nelmess(1955, 1951)对于复序苔草亚属内组的划分也与 Kükenthal(1909)有所不同。

根据 Kükenthal(1909)的记载,全世界复序苔草亚属植物有 61 种,分为 6 组,其中 Sect. *Indicae* 又分为 4 亚组。该亚属主要分布在全世界热带地区,以印度-马来西亚地区种类最多(Ball, 1990);中国长江以南地区种类也很多,约有 30 多种。除 Sect. *Schiedeanae*(两个种分别产于中美和地中海沿岸)在中国没有分布外,其它各组 and 亚组在中国均有代表,Kükenthal(1909)没有记录的 Sect. *Surculosae* 植物在中国亦有分布。

不同时期的学者对苔草属植物营养器官的解剖学研究非常繁多, Metcalf (1971, 1969)和 Standley(1990)都曾对这方面的研究做过总结,他们都认为解剖学资料对于苔草属的系统学研究有重要的参考价值。在他们引用的大量参考文献中,有关复序苔草亚属的资料却很鲜见。许多作者都曾假设复序苔草类植物代表了苔草属中的原始类型(Ball, 1990; Reznicek, 1990; Koyama, 1962; Nelmess, 1952),该亚属无疑是苔草属系统学研究比较关键的类群。作者对产于我国的复序苔草亚属 6 组 4 亚组 14 种代表植物的叶片进行了解剖学研究,观察了其横切面及表皮特征,以期对苔草属的系统学研究积累资料,并据此讨论了复序苔草亚属的一些系统、分类问题。

## 1 材料和方法

试验材料取自中国科学院植物研究所标本馆(PE)收藏的腊叶标本(凭证标本见表 1),均为发育良好的叶片的中间部分。在制备横切面切片时,先将材料在沸水中煮到充分舒展恢复原状,然后放入 FAA 溶液中固定 24 h 以上备用;用实验室常规方法切片、染色,在光学显微镜下观察并拍照。在制备叶片表皮样品时,也需将干材料在沸水中煮约 10 min,再剪成 5 mm 左右的小段,置于 25% 或 10% 的次氯酸钠(NaOCl)溶液中,放入温箱,保持恒温 35 ℃,浸泡 6 h 或 12 h,取出,将材料移入蒸馏水中备用;在解剖镜下仔细剥除叶肉组织,得到叶片的上下表皮,番红染色。在光学显微镜下观察拍照。观察结果的描述使用 Metcalf(1971)的术语。

表 1 材料来源  
Table 1 The origin of materials

Section & Subsection		Species	Voucher
Sect. Japonicae		<i>C. satsumensis</i> Fr. & Sav.	Ohwi 3150 (PE)
Sect. Mundae		<i>C. munda</i> Boott	Xizang Chinese Herb Medician Expedition 331 (PE)
Sect. Polystachyae		<i>C. baccans</i> Nees	Xiong Ji-Hua <i>et al.</i> 33406 (PE)
		<i>C. myosurus</i> Nees	Science Expedition 1612 (PE)
		<i>C. composita</i> Boott	H. T. Tsai 61074 (PE)
Sect. Indicae	Subsect. Turgidulae	<i>C. spatiosa</i> Boott	Huang Zhi 71009 (PE)
		<i>C. cruciata</i> Wahlenb.	Hainan Expedition 745 (PE)
	Subsect. Gracilirostres	<i>C. filicina</i> Nees	Yue Jun-San <i>et al.</i> 4007 (PE)
	Subsect. Hispidulae	<i>C. continua</i> C. B. Clarke	C. W. Wang 79328 (PE)
	Subsect. Scaposae	<i>C. scaposa</i> C. B. Clarke	P. C. Tsoong 187 (PE)
		<i>C. densifimbriata</i> Tang et Wang ex S. Y. Liang	Zhang Zhi-Song <i>et al.</i> 402334 (PE)
Sect. Surculosae		<i>C. kwangsiensis</i> W. & T.	Guangxi Expedition 452 (PE)
		<i>C. tsiangii</i> W. & T.	W. T. Tsiang 20087 (PE)
Sect. Scabrellae		<i>C. moupinensis</i> Fr.	T. T. Yu 749 (PE)

## 2 观察结果

### 2.1 横切面

横切面外形一般为 V 字形,在两侧肋处最厚并且有的外翻形成凸缘(图 1),但 *Carex scaposa* 和 *C. densifimbriata* 为扁平形, *C. tsiangii* 为近扁平形;中脉在远轴面突出,在近轴面形成凹槽(图 1,图 2);近轴面的表皮细胞一般大于远轴面的表皮细胞(图 3);厚壁组织伴随在维管束附近;气腔发育良好,一般大而明显(图 3);叶肉细胞存在于气腔外围,不为辐射状排列(图 3);泡状细胞存在,1 层(图 2);维管束均为外韧维管束,一般较大的和较小的相间排列成一行,横切面呈长圆形至卵形或椭圆形,有的较小的维管束近圆形(图 2,图 3);维管束鞘较明显,由两层细胞构成,外层为薄壁细胞,内层为壁较厚的纤维状细胞(图 2,图 3)。所观察的 14 种植物叶片横切面的性状见表 2。

### 2.2 表皮

从叶片表皮来看,细胞一般为长方形,长轴与叶脉平行,纵向成行排列,细胞垂周壁不同程度地弯曲;端壁平直至弯曲, Sect. Polystachyae 中的 3 个种上表皮细胞的端壁增厚且在表面形成小的乳突(图版 I : 3), *C. continua* 上表皮细胞端壁有圆锥状硅质沉积(图版 I : 6)。所观察的 14 种植物叶表皮上大多无毛, *C. myosurus*, *C. composita* 和 *C. continua* 上表皮有些细胞形成刺状突起, *C. kwangsiensis* 下表皮具单细胞长毛(图版 II : 11);气孔器存在于叶脉之间,都为平列型(两个副卫细胞平行地排列在气孔的两侧),外形

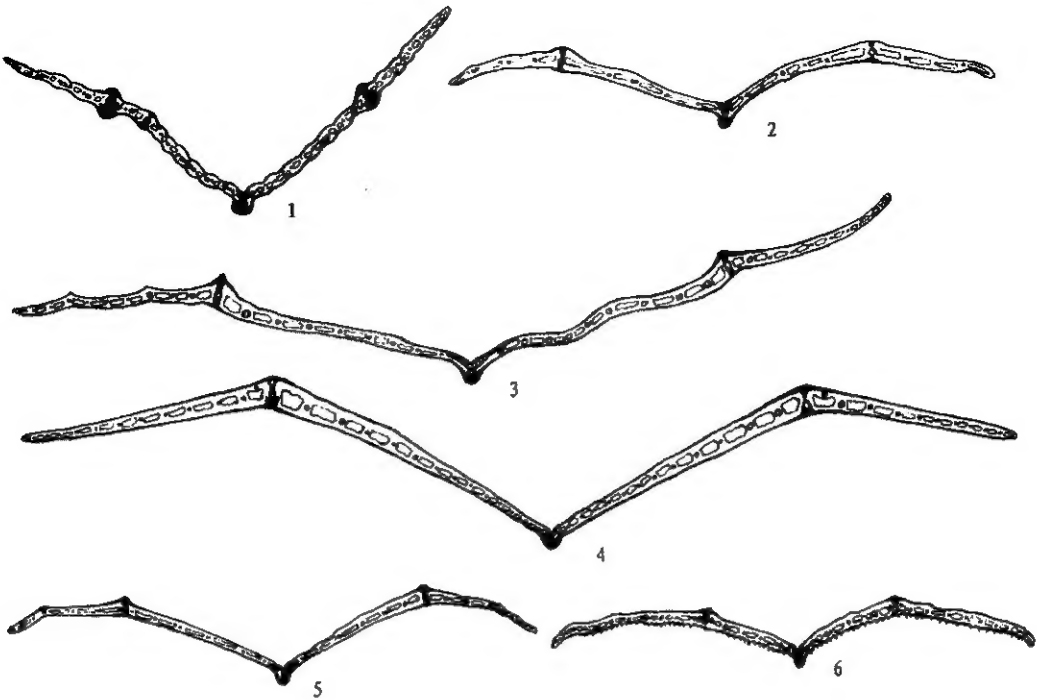


图 1 叶片横切面的形状( $\times 13$ ) (蔡淑琴 绘)

Fig. 1 Outline of transverse section of leaf( $\times 13$ )

1. *Carex baccans* Nees; 2. *C. spatiosa* Boott; 3. *C. cruciata* Wahlenb.; 4. *C. filicina* Nees;  
5. *C. kwangsiensis* Wang et Tang; 6. *C. moupinensis* Franch.

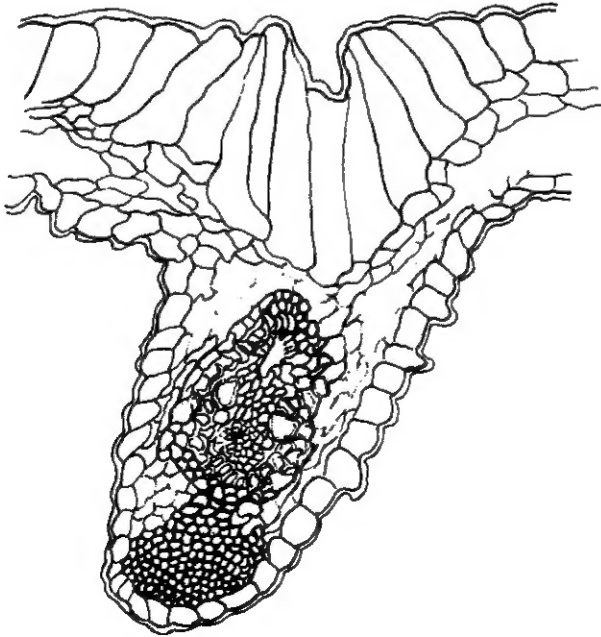
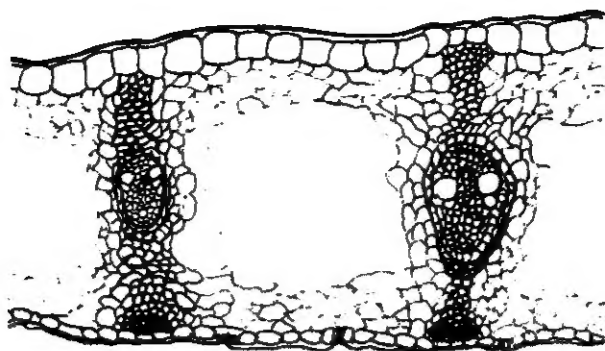


图 2 *Carex spatiosa* Boott 叶片横切面一部分(示中脉,  $\times 160$ ) (蔡淑琴 绘)

Fig. 2 Part of T. S. leaf of *Carex spatiosa* Boott(showing midrib,  $\times 160$ )

表 2 苔草属复序苔草亚属叶片横切面特征  
Table 2 Leaf characters of *Carex* subgenus *Indocarex* at transverse section

Species	Outline	Keel	Median adaxial groove	Epidermis	Air-cavity	Bulliform cell	Number of vascular bundles
<i>C. satsumensis</i>	flanged V-shaped	protruded and acute	shallow and wide	adaxial cells near margins smaller, others equal in size and larger than abaxial ones	large, square or rectangular	inflated and very tall	c. 9 pairs
<i>C. munda</i>	V-shaped	protruded and rounded	well-developed and deep	adaxial cells larger than abaxial ones, cells above veins of both surfaces slightly smaller	very large, rectangular	inflated	c. 8 pairs
<i>C. baccans</i>	V-shaped	protruded and rounded	small	adaxial cells larger than abaxial ones, cells above veins of both surfaces smaller	large, nearly square	well-developed	c. 24 pairs
<i>C. myosurus</i>	flanged V-shaped	protruded and rounded	shallow and wide	adaxial cells larger than abaxial ones, cells above veins of both surfaces smaller	large, rectangular	inflated	c. 22 pairs
<i>C. composita</i>	flanged V-shaped	protruded and rounded	small	adaxial cells larger than abaxial ones, cells above veins of both surfaces smaller	large, nearly square	inflated and tall	c. 15~17 pairs
<i>C. spatiosa</i>	widely V-shaped, slightly flanged	protruded and acute	small	adaxial cells equal in size, much larger than abaxial ones, abaxial cells between veins smaller, some abaxial cells papillose	large, narrowly rectangular	well-developed, very tall and inflated	c. 9 pairs
<i>C. cruciata</i>	widely V-shaped, slightly flanged	protruded and rounded	slight	adaxial cells equal in size, much larger than abaxial ones, abaxial cells above major veins smaller	large, oblong to rectangular	well-developed	c. 23~24 pairs
<i>C. filicina</i>	flanged V-shaped	protruded and rounded	well-developed	adaxial cells much larger than abaxial ones, cells above veins of both surfaces smaller	large, square to rectangular	well-developed	c. 27 pairs
<i>C. continua</i>	widely V-shaped, slightly flanged	protruded and rounded	very shallow and wide	adaxial cells above major veins and near margins smaller, others equal in size and much larger than abaxial ones	large, rectangular	inflated	c. 16 pairs
<i>C. scaposa</i>	flat, and very narrowly elongated	low and rounded	shallow and wide	adaxial cells slightly larger than abaxial ones, cells above veins of both surfaces slightly smaller	large, narrowly rectangular	inflated	c. 24 pairs
<i>C. densifimbriata</i>	flat, and very narrowly elongated	low and rounded	very shallow and wide	adaxial cells slightly larger than abaxial ones, cells above veins of both surfaces smaller	large, narrowly rectangular	inflated	c. 22 pairs
<i>C. kuang-siensis</i>	flanged V-shaped	protruded, sub-rounded	well-developed and wide	adaxial cells equal to or slightly larger than abaxial ones, cells above veins slightly smaller or same, some abaxial cells papillose or hairy	large and oblong	slightly inflated	c. 14 pairs
<i>C. tsiangii</i>	nearly flat	protruded, and acute	small and deep	adaxial cells slightly larger than abaxial ones, cells above major veins smaller, abaxial cells and some adaxial cells slightly papillose	small or large, outlines not well defined	inflated	c. 12 pairs
<i>C. moupinensis</i>	widely V-shaped, slightly flanged	protruded and acute	slight	adaxial cells much larger than abaxial ones, adaxial cells above major veins smaller, abaxial surface papillose	small, outlines not well defined	well-developed, tall and inflated	c. 17~20 pairs

图3 *Carex filicina* Nees 叶片横切面一部分( $\times 200$ ) (蔡淑琴 绘)Fig. 3 Part of T. S. leaf of *Carex filicina* Nees ( $\times 200$ )

一般为椭圆形至长圆形, 少有近圆形, 长轴与叶片长轴平行, 但近轴面上如有气孔器存在则为近圆形。硅质体一般发生在脉上的表皮细胞中。所观察的 14 种植物的表皮性状见表 3。

表 3 苔草属复序苔草亚属叶片表皮特征

Table 3 Epidermal characters of leaves of *Carex* subgenus *Indocarex*

Species	Adaxial surface					Abaxial surface				
	L/B	S	PR	EW	SAW	L/B	SS	H	PA	SAW
<i>C. satsumensis</i>	c. 3	-	-	straight	++	c. 4	broadly elliptic	-	-	++
<i>C. munda</i>	c. 4	-	-	straight, oblique or sinuous	++	c. 4	elliptic	-	-	++
<i>C. baccans</i>	c. 2.5	+	-	incrassated, with small papilla on surface	++	c. 5	elliptic	-	-	++
<i>C. mysurus</i>	c. 3	-	+	incrassated, with small papilla on surface	++	c. 5	elliptic	-	-	++
<i>C. composita</i>	c. 2.5	-	+	incrassated, with small papilla on surface	++	c. 5	oblong-elliptic	-	-	++
<i>C. spatiosa</i>	c. 3	-	-	curved	++	c. 4	oblong	-	-	++
<i>C. cruciata</i>	c. 2.5	-	-	curved or sinuous	++	c. 3	narrowly oblong	-	-	++
<i>C. filicina</i>	c. 2	+	-	straight and sinuous	++	c. 3	elliptic	-	-	++
<i>C. continua</i>	c. 4.5	-	+	straight or curved, with silica deposit	++	c. 5	very narrowly oblong	-	-	++
<i>C. scaposa</i>	c. 1	+	-	very sinuous	+++	c. 1	nearly circular	-	-	+++
<i>C. densifimbriata</i>	c. 1	+	-	very sinuous	+++	c. 1	nearly circular	-	-	+++
<i>C. kwangsiensis</i>	c. 2.5	-	-	sinuous	++	c. 2	broadly elliptic	+	+	+++
<i>C. tsiangii</i>	c. 2	-	-	straight or curved, sometimes sinuous	++	c. 2	broadly elliptic to nearly circular	-	+	+++
<i>C. moupinensis</i>	c. 3	-	-	straight	++	c. 2	broadly elliptic	-	++	+++

L/B = length/breadth of cell; S = stomata: present(+), not seen(-); PR = prickles: present(+), absent(-); EW = end wall; SAW = sinuosity of anticlinal wall: slightly sinuous(+), sinuous(++), seriously sinuous(+++); SS = shape of stomata; H = hairs: present(+), absent(-); PA = papillae: present(++), absent(-), outer wall of cell slightly papillose(+)

### 3 讨 论

#### 3.1 叶片解剖学性状的分类学意义

总体上, 复序苔草亚属这 14 种植物叶片的解剖学性状在气孔器的类型与排列、表皮细胞的形状、维管束类型等方面表现出莎草科植物共有的特征; 与苔草属其它类群在下列性状上也一致: 近轴面细胞大于远轴面细胞, 叶肉中绿色组织不为辐射状排列, 维管束之间存在发育良好的气腔, 泡状细胞发育良好等(cf. Metcalf, 1971)。但是, 从表 2 和表 3 可以看出, 各种植物叶片横切面和表皮解剖学性状存在差异: 从横切面来看, 它们在外形、中脉在远轴面形成的脊和近轴面上的槽、表皮细胞相对大小及角质突起、毛的存在与否、气腔的大小和形状、泡状细胞的性状、侧脉的数目等方面都有所不同; 从叶片表皮来看, 细胞的形状、细胞垂周壁弯曲程度、端壁的性状、气孔器形状、毛被和角质突起等在种与种之间也有变化。同时, 一些近缘种的解剖学性状存在不同程度的相似性, 如 *C. baccans*, *C. myosurus* 和 *C. composita* 叶表皮的特征, *C. scaposa* 和 *C. densifimbriata* 叶片横切面和表皮的特征。可见, 叶片解剖学性状可以做为种及种上等级分类的参考。

#### 3.2 关于复序苔草亚属的系统位置

复序苔草亚属植物叶片的解剖学特征较少特化, 处于较原始的状态。如都为异面叶, 叶片横切面形状都为 V 字形或扁平, 两侧伸长, 纵向很窄, 泡状细胞只有一层, 这些都为较原始的性状(Standley, 1990; Metcalf, 1971)。综合复序苔草亚属植物所共有的较原始的外部形态性状: 囊状的枝先出叶、复杂的圆锥花序、全部小穗两性而为雄雌顺序等, 作者认为复序苔草亚属植物代表了苔草属中较原始的类型。

#### 3.3 关于分组的意见

*C. baccans*、*C. myosurus* 和 *C. composita* 属于 Sect. *Polystachyae* (Kükenthal, 1909), 其叶片解剖学特征的诸多性状非常一致, 如中脉在横切面的突出部分圆钝、上表皮细胞较大而为长方形(长/宽=2.5~3), 且端壁增厚并在表面形成小的乳突、下表皮细胞较小而为狭长方形(长/宽=5)等。Sect. *Indicae* 中的种类叶片解剖学性状已有分化, 其中 *C. cruciata* 并不与同亚组的 *C. spatiosa* 相近, 反而与 *C. filicina* 相似; *C. continua* 因上表皮细胞端壁有硅质沉积、下表皮细胞狭长及气孔器狭矩圆形而较为独特; *C. scaposa* 和 *C. densifimbriata* 因叶片横切面扁平、上下表皮细胞近方形、垂周壁在叶表面强烈弯曲、气孔器近圆形而与所观察的 14 种植物都不同。

综上所述, 我们支持 Kükenthal(1909)对 Sect. *Polystachyae* 的划分; 但是 Sect. *Indicae* 的划分及其中亚组的分类值得商榷。*C. cruciata* 与 *C. spatiosa* 归类于 Subsect. *Turgidulae* 不尽合理, 前者与 Subsect. *Gracilirostres* 中的 *C. filicina* 更相近; *C. continua* 应为一单独的类群, 但给予什么等级、与哪些种较近缘需进一步研究; *C. scaposa* 和 *C. densifimbriata* 与所观察的其它植物区别显著, 加之上述二种及其近缘类群具有狭椭圆形的叶片及侧生的秆, 外形独特, 因此作者同意 Raymond(1959)和 Nelves(1955)的处理, 将其做为复序苔草亚属中的一个组 Sect. *Hemiscaposae* C. B. Clarke 而非亚组 Subsect. *Scaposae* Kükenthal。

致谢 本文插图由蔡淑琴先生绘制, 谨此致谢。



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## 图版说明 Explanation of plates

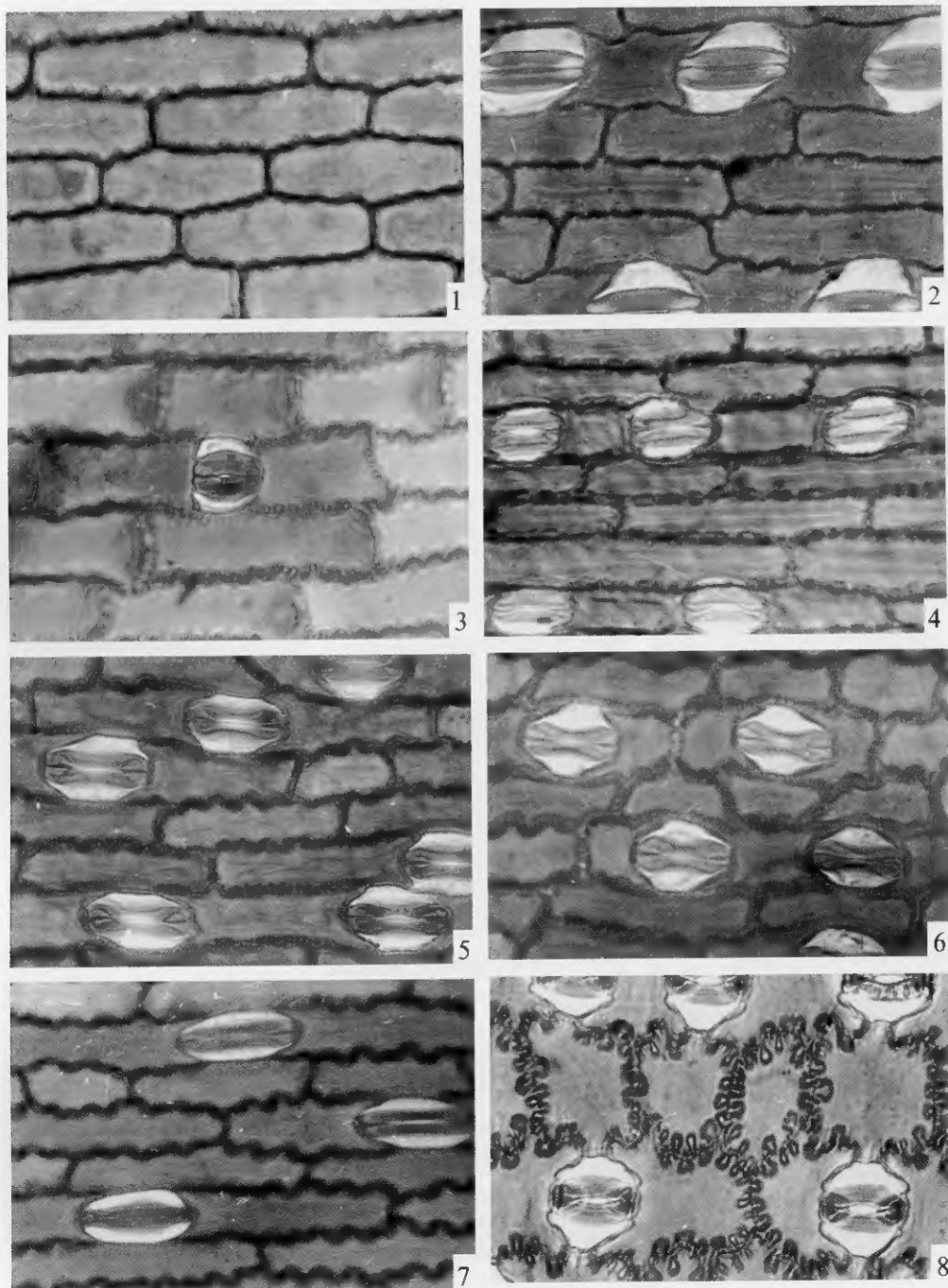
**图版 I** 叶片的表皮( $\times 320$ ): 1, 3. 上表皮; 2, 4~8. 下表皮 1~2. *Carex satsumensis* Franch. et Sav.; 3. *C. baccans* Nees; 4. *C. spatiosa* Boott; 5. *C. cruciata* Wahlenb.; 6. *C. filicina* Nees; 7. *C. continua* C. B. Clarke; 8. *C. scaposa* C. B. Clarke.

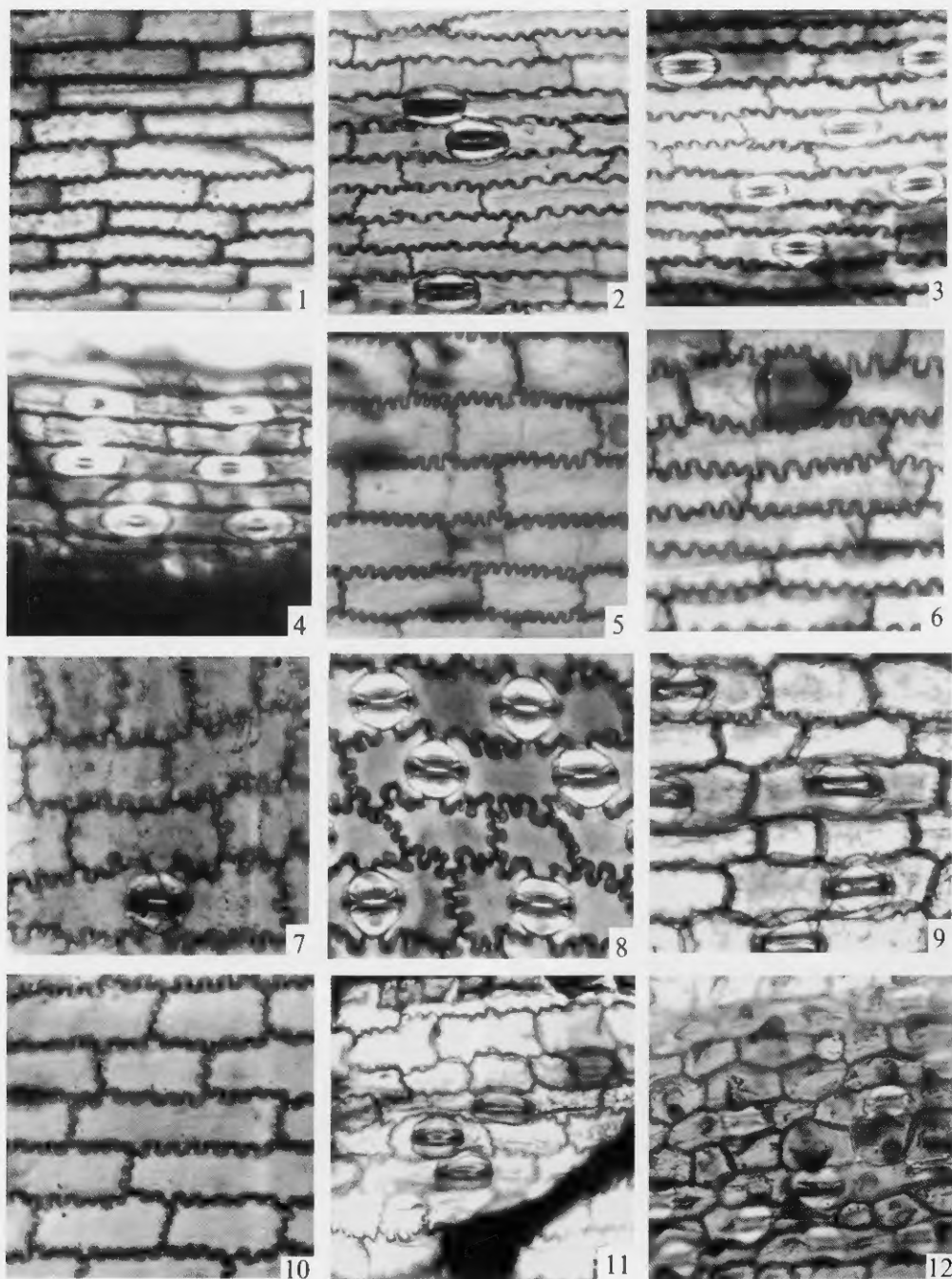
**图版 II** 叶片的表皮( $\times 256$ ): 1, 5~7, 10. 上表皮; 2~4, 8, 9, 11, 12. 下表皮 1~2. *C. munda* Boott; 3. *C. myosurus* Nees; 4. *C. composita* Boott; 5. *C. cruciata* Wahlenb.; 6. *C. continua* C. B. Clarke; 7~8. *C. densifimbriata* Tang et Wang ex S. Y. Liang; 9. *C. tsiangii* Wang et Tang ex P. C. Li; 10~11. *C. kwangsiensis* Wang et Tang ex P. C. Li; 12. *C. moupinensis* Franch.

**Plate I** Epidermis of lamina( $\times 320$ ): 1, 3. adaxial; 2, 4~8. abaxial 1~2. *Carex satsumensis* Franch. et Sav.; 3. *C. baccans* Nees; 4. *C. spatiosa* Boott; 5. *C. cruciata* Wahlenb.; 6. *C. filicina* Nees; 7. *C. continua* C. B. Clarke; 8. *C. scaposa* C. B. Clarke.

**Plate II** Epidermis of lamina( $\times 256$ ): 1, 5~7, 10. adaxial; 2~4, 8, 9, 11, 12. abaxial 1~2. *C. munda* Boott; 3. *C. myosurus* Nees; 4. *C. composita* Boott; 5. *C. cruciata* Wahlenb.; 6. *C. continua* C. B. Clarke; 7~8. *C. densifimbriata* Tang et Wang ex S. Y. Liang; 9. *C. tsiangii* Wang et Tang ex P. C. Li; 10~11. *C. kwangsiensis* Wang et Tang ex P. C. Li; 12. *C. moupinensis* Franch.







See explanation at the end of text